Trophic coherence determines food-web stability

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Abstract. The fact that large, complex ecosystems are particularly robust is mysterious in the light of mathematical arguments that suggest they should be unstable; i.e., susceptible to runaway fluctuations in species' abundances. Here we show that food webs (networks describing who eats whom in an ecosystem) exhibit a property we call trophic coherence, a measure of how neatly the species fall into distinct levels. We find that this property makes networks far more linearly stable than if the links (predator - prey interactions) were placed randomly between species, or according to existing structural models. A simple model we propose to capture this feature shows that networks can, in fact, become more stable with size and complexity, suggesting a possible solution to the paradox.

1   Introduction

In the early seventies, Robert May addressed the question of whether a generic system of coupled dynamical elements randomly connected to each other would be stable. He found that the larger and more interconnected the system, the more difficult it would be to stabilize. May's deduction followed from the behavior of the leading eigenvalue of the interaction matrix, which, in a randomly wired system, grows with the square root of the mean number of links per element.

This result clashed with the received wisdom in ecology - that large, complex ecosystems were particularly stable - and initiated the "diversity - stability debate". This seems incongruous with a general mathematical principle that "complexity begets instability", and has become known as Mays paradox. One solution might be that the linear stability analysis used by May and many subsequent studies does not capture essential characteristics of ecosystem dynamics, and much work has gone into exploring how more accurate dynamical descriptions might enhance stability. However, as ever - better ecological data are gathered, it is becoming apparent that the leading eigenvalues of matrices related to food webs (networks in which the species are nodes and the links represent predation) do not exhibit the expected dependence on size or link density. Food webs must, therefore, have some unknown structural feature that accounts for this deviation from randomness - irrespectively of other stabilizing factors.

2 Measuring Stability

Let us assume that the populations of species making up an ecosystem (each characterized by its total biomass) change through time according to some set of nonlinear differential equations, the interactions determined by the predation matrix, A (whose elements a_{ij} take the value 1 if species i preys on species j, and 0 otherwise). If the system persists without suffering large changes it must, one assumes, find itself in the neighborhood of a fixed point of the dynamics. We can study how the system would react to a small perturbation by expanding the equations of motion around this fixed point and keeping only linear terms. The subsequent effect of the perturbation is then determined by the corresponding Jacobian matrix, and the system will tend to return to the fixed point only if the real parts of all its eigenvalues are negative.

Even without knowledge of the details of the dynamics, it is possible to draw some conclusions about the stability of a food web solely from its predation matrix. Independently of the exact interaction strengths, we know that not all of the biomass lost by a prey species when consumed goes to form part of the predator; in fact, this efficiency is relatively low. It is therefore natural to assume that the effect of species j on species i will be mediated by $w_{ij} = \eta a_{ij} a_{ji}$, where η is an efficiency parameter that, without further information, we can consider equal for all pairs of species. We can thus treat the interaction matrix $W = \eta A - A^T$ as the Jacobian of some unspecified dynamics.

Therefore, the eigenvalue with largest real part of W, as defined above, can be seen as a measure of the minimum intraspecies competition required for the system to be stable. Thus, the lower this value, $R = Re(\lambda_1)$, the higher the stability.

This measure of stability depends on the parameter η. However, the results reported here remain qualitatively unchanged for any $\eta \in (0, 1)$. For the results in the main text we use the fixed value $\eta = 0.2$.

3 Trophic Coherence

Each species in an ecosystem is generally influenced by others, via processes such as predation, parasitism, mutualism, or competition for various resources. A food web is a network of species that represents the first kind of influence with directed links from each prey node to its predators. Such representations can therefore be seen as transport networks, where biomass originates in the basal species (the sources) and flows through the ecosystem, some of it reaching the apex predators (the sinks).

The trophic level of a species s_i of species i can be defined as the average trophic level of its prey, plus 1. Thus, plants and other basal species are assigned level 1, pure herbivores have level 2, but many species will have fractional values. A species trophic level provides a useful measure of how far it is from the sources of biomass in its ecosystem. In order to compute it, we have:

$$s_i = 1 + \frac{1}{k_i^{in}} \sum_j a_{ij} s_j$$

where $k_i^{in} = \sum_j a_{ij}$ is the number of prey of species i (or is in degree), and a_{ij} are elements of the predation matrix A. Basal species (those with $k_{in} = 0$) are assigned $s = 1$. The trophic level of each species is therefore a purely structural property that can be determined by solving a system of linear equations. We can write the linear system in terms of a modified graph Laplacian matrix, $\Delta \mathbf{s} = \mathbf{v}$, where $\mathbf{s}$ is the vector of trophic levels, $\mathbf{v}$ is the vector with elements $\mathbf{v}_i = max(k_i^{in}, 1)$, and $\Delta = diag(\mathbf{v}) - A$. Thus, every species can be assigned a trophic level if and only if Δ is invertible. This requires at least one basal species (else zero would be an eigenvalue of Δ).

We can characterize each link in a network with a trophic distance, defined as the difference between the trophic levels of the predator and prey species involved. We define the trophic distance spanned by each link $(a_{ij} = 1)$ as $x_{ij} = s_i - s_j$ (which is not a distance in the mathematical sense because it can take negative values).

We then look at the distribution of trophic distances over all links in a given network. The mean of this distribution, by definition, will always be equal to 1, and we refer to its degree of homogeneity as the networks trophic coherence. We shall measure this degree of order with the standard deviation of the distribution of trophic distances, $q = \sqrt{\langle x \rangle - 1}$, where $\langle \cdot \rangle = L^{-1} \sum_{ij} (\cdot) a_{ij}$, and L is the total number of links, $L = \sum_{ij} a_{ij}$. A perfectly coherent network, in which all distances are equal to 1 (implying that each species occupies an integer trophic level), has $q = 0$, and less coherent networks have $q > 0$. We therefore refer to this q as an incoherence parameter.

4 Stability Results

A fundamental property of ecosystems is their ability to endure over time. "Stability" is often used as a generic term for any measure of this characteristic, including for concepts such as robustness and resilience. When the analysis regards the possibility that a small perturbation in population densities could amplify into runaway fluctuations, stability is usually understood in the sense of Lyapunov stability, which in practice tends to mean linear stability. This is the sense we shall be interested in here, and henceforth stability will mean linear stability. Even without precise knowledge of the dynamics, one can still learn about the stability of a system just from the network structure of interactions between elements (in this case, species whose trophic interactions are described by a food web). We have described how an interaction matrix W can be derived from the adjacency (or predation) matrix A representing a food web, such that the real part of Ws leading eigenvalue, $R = Re(\lambda_1)$, is a measure of the degree of self-regulation each species would require in order for the system to be linearly stable. In other words, the larger R, the more unstable the food web.

May considered a generic Jacobian in which link strengths were drawn from a random distribution, representing all kinds of ecological interactions. Because, in this setting, the expected value of the real part of the leading eigenvalue (R) should grow with $\sqrt{SC}$, where S is the number of species and C the probability that a pair of them be connected, larger and more interconnected ecosystems should be less stable than small, sparse ones.

We analyze the stability for each of a set of 46 empirical food webs from several kinds of ecosystem. In Fig. 1A we plot the R of each web against $\sqrt{S}$, observing no significant correlation. Fig. 1B shows R against $\sqrt{K}$, where $K = SC$ is a networks mean degree (often referred to as complexity). We observe a positive correlation between R and $\sqrt{K}$. However, less than half the variance in stability can be accounted for in this way. In Fig. 1C we plot R for the same food webs against the incoherence parameter q. The correlation is significantly stronger than with complexity - stability increases with coherence. In other words, trophic coherence account for 60% of the variation in stability observed in this dataset.
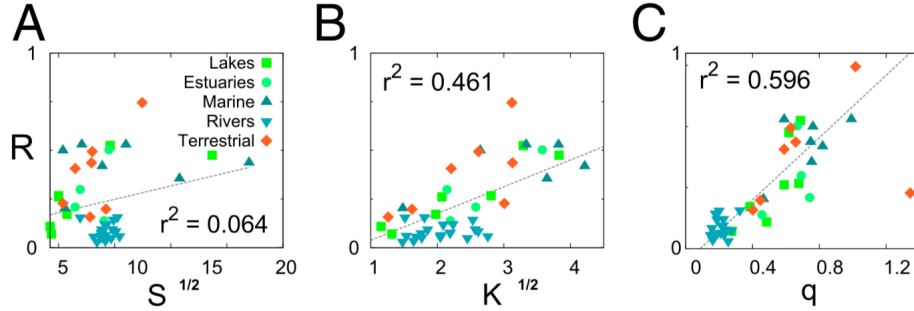

Fig. 1. Scatter plots of stability (as measured by R, the real part of the leading eigenvalue of the interaction matrix) against several network properties in a dataset of 46 food webs; Pearsons correlation coefficient is shown in each case. (A) Stability against $\sqrt{S}$ where S is the number of species ($r^2 = 0.064$). (B) Stability against $\sqrt{k}$ where K is the mean degree ($r^2 = 0.461$). (C) Stability against incoherence parameter q ($r2 = 0.596$).

5   Modeling Food-Web Structure

Many mathematical models have been put forward to simulate various aspects of food webs. These models produce networks with many of the statistical properties of food webs. However, they tend to predict significantly less trophic coherence (larger q) than we observe in our dataset. We therefore propose the preferential preying model (PPM) as a way of capturing this feature.

We begin with B nodes (basal species) and no links. We then add, sequentially, $S-B$ new nodes (consumer species) to the system according to the following rule. The first prey species is chosen randomly, and the rest are chosen with a probability that decays exponentially with their absolute trophic distance to that initial prey species (i.e., with the absolute difference of trophic levels). This probability is set by a parameter T that determines the degree of trophic specialization of consumers. The number of prey is drawn from a beta distribution with a mean value proportional to the number of available species.

The computation goes as follows. A new node i is first awarded a random node j from among all those available when it arrives. Then another κ_i nodes l are chosen with a probability P_{il} that decays with the trophic distance between j and l. Specifically, we use the exponential form:

$$P_{il} \propto exp\Big(-\frac{|s_j - s_i|}{T}\Big)$$

where j is the first node chosen by i, and T is a parameter that sets the degree of trophic specialization of consumers. The number of extra prey is $\kappa_i = x_i n_i$, where n_i is the number of nodes already in the network when i arrives, and x_i is a random variable drawn from a beta distribution with parameters $\beta = \frac{S^2 - B^2}{2L} - 1$, where L is the expected number of links. Once i has been assigned all its prey, s_i is updated to its correct value.

The PPM assumes that if a given species has adapted to prey off species A, it is more likely to be able to consume species B as well if A and B have similar trophic levels than if not. The trophic level of a node is defined by the emerging network architecture itself.

Fig. 2 shows three networks with varying degrees of trophic coherence. The one on the left was generated with the PPM and $T = 0.01$, and because it falls into perfectly ordered, integer trophic levels, it is maximally coherent, with $q = 0$. For the one on the right we have used $T = 10$, yielding a highly incoherent structure, with $q = 0.6$.
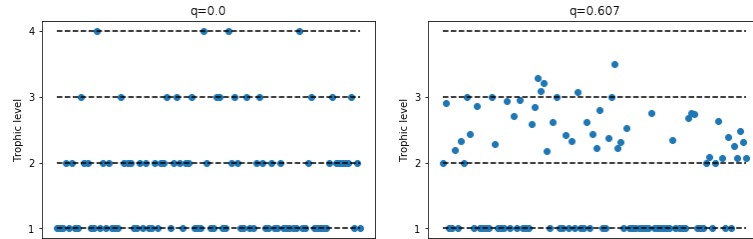

Fig. 2. Two networks generated with the PPM with differing trophic coherence, the height of each node representing its trophic level. The networks on the left and right were generated with $T = 0.01$ and $T = 10$ yielding a maximally coherent structure ($q = 0$) and a highly incoherent one ($q = 0.607$), respectively. Both have the same numbers of species, basal species, and links.

Fig. 3 shows how trophic coherence varies with T in PPM networks and the stability, as measured by R, the leading eigenvalue of the interaction matrix. For the PPM networks, stability closely mirrors trophic coherence: as T decreases, the networks become more stable (smaller R) as well as more coherent (smaller q).
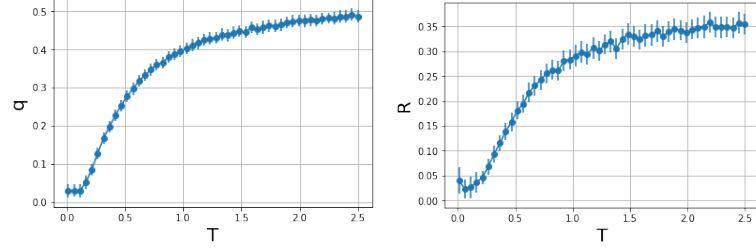

Fig. 3. Left: Incoherence parameter q and **Right:** stability as given by R, the real part of the leading eigenvalue of the interaction matrix, against T, averaged over one hundred networks for each value of T.

6   Conclusions

The predation matrices corresponding to real ecosystems are clearly peculiar in some way, because their largest eigenvalues do not depend solely on their size or complexity, as we would expect both from random graph theory and structural food-web models. This is in keeping with the empirical observation that large, complex ecosystems are particularly stable, but challenges current thinking on food-web architecture. We have shown that the structural property we call trophic coherence is significantly correlated with food-web stability. We have suggested the preferential preying model as a simple algorithm for generating networks with tunable trophic coherence.

Further work show that our model predicts that networks should become more stable with increasing size and complexity, as long as they are sufficiently coherent and the number of links does not grow too fast with size. If stability decreased with size and complexity, as previous theoretical studies have assumed, ecosystems could not grow indefinitely, for they would face a cutoff point beyond which they would become unstable. On the other hand, if real ecosystems are coherent enough that they become more stable with size and complexity, as our model predicts, then the reverse might be true. We must also bear in mind, however, that our results are only for linear stability, whereas structural stability, for instance, may depend differently on size and coherence, and could become the limiting factor.